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REVIEWS

The evolution of mutual ornamentation

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Many conspicuous ornamental traits in animals are expressed in both males and females. Despite this, most research has focused on sexually dimorphic ornamentation. Mutual ornamentation has often been viewed as a result of either a nonadaptive genetic correlation between the sexes or similar selection pressures in both sexes. Here, we review the theoretical underpinning and empirical evidence for these ideas. Few studies have attempted to test empirically whether a genetic correlation between the sexes can constrain the evolution of sexual dimorphism, and the results have been mixed. By contrast, there is good evidence that mutual ornaments can have a signal function in both sexes, especially in terms of mate choice. Other possible signalling functions have received little attention. Social status signalling is especially likely to be important, because competition over nonsexual resources is more balanced between the sexes than sexual competition. There is a need for experimental studies that explicitly test these hypotheses simultaneously in both sexes.

Keywords: genetic correlation; meta-analysis; mutual ornamentation; mutual sexual selection; social selection

Recent decades have seen a surge of interest into elaborate ornamentation resulting from sexual selection. The overwhelming majority of these studies focused on sexually dimorphic ornamentation. In fact, sexually selected ornaments are often defined in terms of sexual dimorphism (e.g. Andersson 1994). This emphasis on sexual dimorphism disregards the fact that both males and females are ornamented in many species, often to a very similar degree. The aim of this review is to assess what factors are involved in the evolution and maintenance of such mutual ornamentation.

Two hypotheses have been proposed to explain elaborate ornamentation in both sexes. The genetic correlation hypothesis states that elaborate monomorphic characters are functional in only males (e.g. as mate choice or status signals), while the corresponding elaborate female characters are nonfunctional and expressed as by-products arising from genetic correlation between the sexes (Lande 1980, 1987; Rice 1984). The mutual selection hypothesis proposes that elaborate monomorphic characters are the result of selection for their expression in both sexes (Huxley 1914; West-Eberhard 1979; Johnstone et al. 1996; Johnstone 1997). Three processes may select for ornamentation in both males and females, namely mate choice and mate competition (mutual sexual selection), social competition over resources other than mates (social selection), and selection for sexual mimicry. While we present these processes separately, it is important to realize that they are not alternatives, but are all part of a social signalling mechanism. Any signal trait may thus be used in contests over mates, in contests over nonmate resources and in mate choice, all simultaneously (e.g. Berglund et al. 1996).

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DATA COLLECTION AND META-ANALYSIS

We searched the literature for studies investigating the signal function of ornaments that are expressed in both sexes, either to a similar degree in males and females or to a reduced degree in females as compared to males.

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Specifically, we searched literature databases (Web of Science) and the reference lists in relevant papers (e.g. Bonduriansky 2001). We defined ornaments as any signal trait that is elaborated to such a degree that its cost is greater than required by efficacy (i.e. a handicap; Zahavi 1975; Maynard Smith & Harper 2003). However, assessing whether or not the cost of a trait under investigation exceeds its efficacy cost is difficult, and we, therefore, include any trait that can reasonably be said to be conspicuous. In some cases the cost of the ornament in terms of natural selection may be neutral, or even weakly positive, for example tail-streamers in birds (Veit & Jones 2003), or eye-stalks in diopsid flies (Burkhardt & de la Motte 1985). Nonornamental traits that are often involved in mate choice, such as body size, were excluded.

To analyse the results of the studies quantitatively, we carried out a meta-analysis using MetaWin version 2 (Rosenberg et al. 2000). To be included in the meta-analysis, a study had to report a statistical measure (with sample size) of association between the level of ornament expression in females or both males and females, and the parameter of interest (component of fitness, age, mate preference, social dominance). Studies that only investigated male signals were excluded. Since most of the studies in this analysis were correlational, we used correlation coefficients (r) as our measure of effect size. When a primary study reported an F, t or χ^2 statistic instead of r, we converted this value to an r using the MetaWin Statistical Calculator (Rosenberg et al. 2000). If none of these values were reported, but a one-tailed P value was available, we calculated the standard normal deviate and converted this to r using MetaWin Statistical Calculator. The sign of the correlation coefficients for timing of breeding was reversed as the predicted relationship is negative. With these correlation coefficients, MetaWin estimates effect sizes using Fisher's Z-transformation. Mean effect size and its surrounding confidence intervals calculated in MetaWin by a bootstrap randomization procedure with 999 iterations. We considered the mean effect size across studies to be significant when the 95% confidence interval around the Fisher's Z did not include zero. Many studies reported results for multiple ornaments and some multiple measurements for the same ornament (e.g. eye hue, eye saturation; Massaro et al. 2003). Because different ornaments within the same species cannot be considered independent, we used the weighted mean for all ornaments in a species as the independent variable. The data were grouped by ornament type (body colour, structure size, integument colour), whether age was accounted for, and fitness parameter (timing of breeding, parental investment, reproductive success, body condition, parasite resistance, survival). Because our criteria for including studies were broad (e.g. both experimental and correlational) we exclusively used random effect models, which incorporate a random component of variation in effect sizes between studies (Rosenberg et al. 2000). We report the total heterogeneity (Q_{tot}) for each analysis. Since these were never statistically significant, we did not explore whether other factors explained any of the variation in effect sizes among studies, except for the effect of correcting for age. To investigate the effect of correcting for age, we used MetaWin to create models that included this variable and report Q_b, the between-groups homogeneity. Last, we investigated whether there was publication bias (i.e. whether nonsignificant results were less likely to be published) by testing for a correlation between the standardized effect size of each study and the sample size (note that this test has low statistical power).

ELABORATE ORNAMENTATION ARISING FROM GENETIC CORRELATION BETWEEN THE SEXES

The genetic correlation hypothesis proposes that females gain no selective benefits from the expression of elaborate characters. In a now classic paper, Lande (1980) modelled the evolution of sexual dimorphism (Fig. 1a). During the initial (rapid) phase the sexes evolve in parallel as a consequence of sexual selection on males. Strong genetic correlations (primarily due to pleiotropy) result in selective

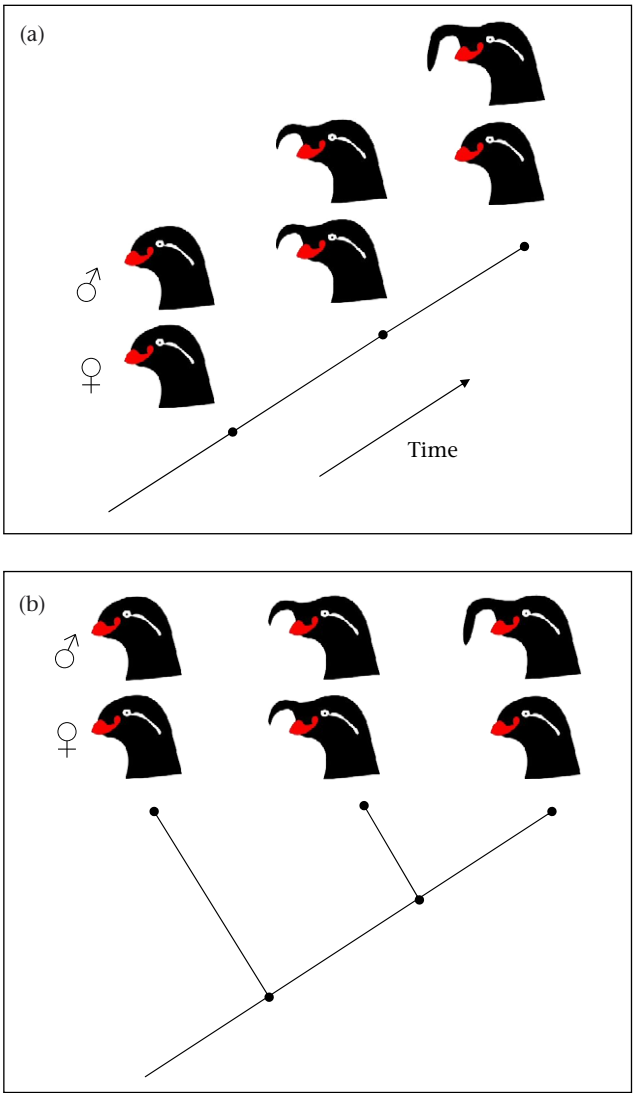

Figure 1. (a) Hypothetical scenario for the evolution of sexual dimorphism from a dull monomorphic ancestor (Lande 1980). (b) If the process depicted in (a) is sufficiently slow, it could potentially be traced on phylogenies of extant taxa.

compromises in males and females, such that the mean fitness of one sex is temporarily decreased. This phase persists until the net selective forces on the sexes become nearly equal in magnitude, but opposite in sign. During the second phase, the sexes gradually evolve in response to their own selective forces. The sexes can thus evolve towards their separate optima: a return to lower expression in females and continued selection for higher expression in males (Fig. 1a). When female mate choice was allowed to evolve in the model this did not change the above scenario (Lande & Arnold 1985). In these models, species always passed through a mutually ornamented stage during their evolution towards sexual dimorphic ornamentation (Fig. 1a). Mutually ornamented species are expected to be in the first phase: sexual selection for male ornamentation has started recently and not enough time has passed for the ornament to become sexually dimorphic. Therefore, the genetic correlation explanation for mutual ornamentation is sometimes referred to as 'phylogenetic inertia' (Trail 1990). In this state, genes coding for the ornament are expected to be under sexually antagonistic selection pressures: males are selected for increased ornament size, while females are selected for decreased ornament size. Studies in *Drosophila* have shown substantial sexually antagonistic fitness variation (Chippindale et al. 2001). When selection on females was experimentally eliminated, the fitness of males increased, while that of females decreased (Rice 1998). These results suggest that sexually antagonistic alleles are common, and thus that complete sex limitation may take long to evolve.

Experimental evidence for the idea that female ornament expression may be increased through a genetic correlation with males comes from an artificial selection experiment in the stalk-eyed fly *Cyrtodiopsis dalmanni*. Eyespan in this species is a sexually selected trait (Burkhardt & de la Motte 1988; Wilkinson & Reillo 1994; Panhuis & Wilkinson 1999). Artificial selection on male eyespan resulted in a correlated response in female eyespan (Wilkinson 1993), suggesting that the two are genetically correlated. However, this conclusion is equivocal because mating patterns were not controlled for in the experiment (Butlin 1993). If large-eyespan males prefer to mate with large-eyespan females, the result could be due to direct sexual selection on females, rather than a genetic correlation between the sexes. Harrison (1953) selected male and female *Drosophila melanogaster* in opposing directions for abdominal bristle number, a sexually dimorphic trait with females normally expressing higher numbers than males. Selection was either in the same direction as the naturally occurring dimorphism (females higher and/or males lower; six lines), or towards decreased sexual dimorphism (females lower and/or males higher; six lines). In four lines a response to selection was observed in both sexes, while only one was being selected away from the mean value. In two of the decreased dimorphism lines, there was a reversal of sexual dimorphism, yet in the remaining lines no change in dimorphism was evident. Genetic correlations between males and females thus resulted in selective compromises rather than independent responses.

Table 1. Estimates for the genetic correlation between the sexes (r) for ornamental traits from parent–offspring regression

Species	Scientific name	Trait	r	N	Experimental design	Source
Barn owl	*Tyto alba*	Plumage spottiness	0.79	141	Cross-fostering	Roulin et al. 2001a
Barn swallow	*Hirundo rustica*	Tail length	0.54	57	Unmanipulated	Møller 1993
Zebra finch	*Taeniopygia guttata*	Bill colour	0.91	43	Unmanipulated	Price & Burley 1993
		Bill colour	0.81	22	Cross-fostering	Price 1996
Stalk-eyed fly	*Cyrtodiopsis dalmanni*	Eye-stalk length	0.29	40	Artificial selection	Wilkinson 1993
Fruit fly	*Drosophila serrata*	5,9-Pentacosadiene	0.71	42	Paternal half-sib	Chenoweth & Blows 2003
		9-Pentacosane	−0.09	42	Paternal half-sib	Chenoweth & Blows 2003
		9-Hexacosane	0.23	42	Paternal half-sib	Chenoweth & Blows 2003
		2-Methylhexacosane	0.85	42	Paternal half-sib	Chenoweth & Blows 2003
		5,9-Heptacosadiene	0.53	42	Paternal half-sib	Chenoweth & Blows 2003
		2-Methyloctacosane	−0.15	42	Paternal half-sib	Chenoweth & Blows 2003
		5,9-Nonacosadiene	0.65	42	Paternal half-sib	Chenoweth & Blows 2003
		2-Methyltriacontane	0.32	42	Paternal half-sib	Chenoweth & Blows 2003

Several quantitative genetic studies estimated the genetic correlation between the sexes (r) for ornamental traits (Table 1). The mean Fisher's Z for these studies was significantly different from zero (0.65, 95% confidence interval: 0.34–0.96). The total amount of heterogeneity in effect size among these studies was not significant ($Q_{tot,12} = 12.27$, $P = 0.42$). Thus, these studies show that ornamental traits can be genetically correlated between the sexes. Whether this can result in maladaptive ornament expression in females as predicted by the genetic correlation hypothesis is less clear. The degree to which genetic correlations prevent the sexes from independent evolution can only be assessed directly when the selection gradients on these traits are known for each sex. Chenoweth & Blows (2003) measured both the sex-specific sexual selection gradients and the intersex genetic correlation in eight cuticular hydrocarbons (CHCs, chemical compounds that play an important role in mate choice in insects and can be seen as pheromonal 'ornaments'; Table 1), but found none for which the genetic correlation was strong and the selection gradients opposing for males and females. In contrast, a quantitative genetic study on the zebra finch provides compelling evidence that a genetic correlation between the sexes can retard the evolution of sexual dichromatism in bill colour (Price 1996). Using a cross-fostering experiment, Price (1996) showed that there is a strong genetic correlation between the sexes for bill colour ($r = 0.81$). Selection differentials from a free-flight aviary experiment were positive for males, but negative for females, indicating that males are selected for redder bill, but females for less red bills (Price 1996). Combining these results with estimates for heritability, Price (1996) was able to show that the genetic correlation between the sexes creates a genetic load that prevents both sexes from evolving towards their separate selective optima. Given the lack of further quantitative genetic studies, it is difficult to assess the generality of this finding.

Genetically, the transition towards sexual dimorphism may proceed in at least two ways (Rice 1984). First, there may be an increase in frequency of genes that enhance trait size in males but not in females. This requires that new mutations are sex-limited in expression (e.g. by being located on the sex chromosomes) and is therefore restrictive. Second, there may be an increase in frequency of genes that enhance trait size in both sexes followed by the evolution of modifier genes that restrict the expression to one sex. In this case sexual dimorphism is achieved through sex-linked loci that suppress the ornament expression in females, not through a reduction in genetic correlation in ornament genes themselves (Fig. 2). The modifier genes need not be new, but can include the co-option of existing genes that modify other sexual functions to achieve sex-linked expression of the ornament. In many birds, for example, ornamental male-type plumage depends on the absence of oestrogen or the presence of either testosterone or luteinizing hormone (Owens & Short 1995; Kimball & Ligon 1999). This shows that the genes coding for the ornament are present in females, but are suppressed under normal circumstances through the action of hormones. Sometimes, selection on other traits that are affected by the threshold

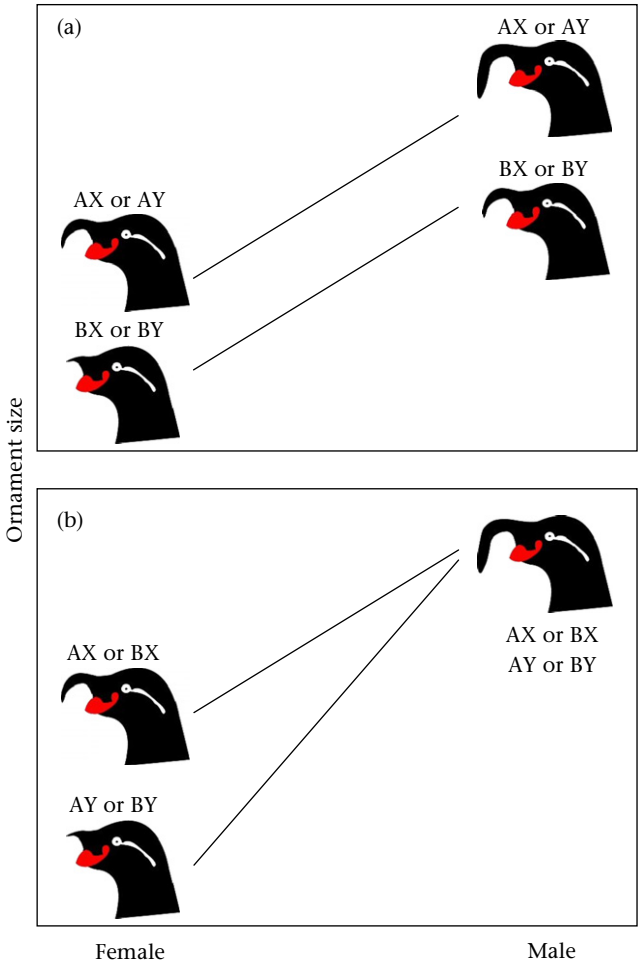

Figure 2. The effect of genetic correlation between the sexes on ornament expression in males and females of a sexually dimorphic species. The ornament itself is produced by an autosomal gene, of which there are two alleles (A and B). A sex-linked modifier gene reduces trait size in female, but not in males. This gene also has two alleles (X and Y). (a) Allelic variation in the autosomal gene influences ornament size in both males and females (allele A produces a large ornament, allele B a smaller ornament). In both cases the sex-linked modifier gene reduces the size of the ornament in females to the same extent. Although the modifier gene has sex-specific effects it does not contribute any intersexual genetic covariance because each allele has the same phenotypic effect. The genetic correlation between the sexes equals 1. (b) Allelic variation in the sex-linked modifier gene causes female ornament size to vary independently of male ornament size. Allele X reduces the female ornament by 50%, allele Y reduces it by 80%. In this case the genetic correlation between the sexes is less than 1.

mechanism may result in a shift in hormone levels and cause the gain of female ornamentation as a maladaptive pleiotropic effect (Emlen et al. 2005a).

Sex-linked inheritance and sex-specific modification may be involved in the development of different ornaments within the same species. Chenoweth & Blows (2003) measured the genetic correlation between the sexes for eight sexually selected CHCs in the fruit fly *Drosophila serrata*. The results showed that X-linked loci allowed largely independent expression of three of the CHCs in

males and females (Chenoweth & Blows 2003). In two other CHCs the autosomal and total additive genetic correlations were both low, and their expression highly sexually dimorphic, indicating that their expression was under independent genetic control in males and females. However, comparative work indicates that sex-linked modification of ornament expression is more common than sex-linked inheritance of ornament genes (Wiens 2001; Emlen et al. 2005b). The sex-linked modifier mechanism predicts that when selection against ornament expression in females of sexually dimorphic species is reduced, the male-type ornament should re-appear. Furthermore, when females of sexually dimorphic species secondarily come under selection for ornamentation they should be pre-adapted to develop the same ornament as the male, rather than a novel ornament (West-Eberhard 2003). Phylogenetic studies have shown that this predicted pattern of a secondary gain of an ornament in females that is already present in males is common (reviewed in Wiens 2001). The situation where both males and females are ornamented, but have different ornaments appears to be rare (e.g. Heinsohn et al. 2005). For example, a comparative study of male and female ornamentation in dung beetles of the genus *Onthophagus* found 13 independent evolutionary gains of female ornamentation, but only one of these involved a female ornament that was different from that in males of the same species (Emlen et al. 2005b). Comparative studies also suggest that sex-linked modifier mechanisms that suppress ornament expression in females can be gained and lost relatively easily (Price & Birch 1996; Wiens 2001). Specifically, it has been shown that over evolutionary history, elaborate characters in one sex can change independently of the direction of change in the other sex (Figuerola & Green 2000; Ord & Stuart-Fox 2005), and that changes in characters from drab to colourful (and in the other direction) have occurred much more frequently in females than in males in several groups (Irwin 1994; Burns 1998). However, it is far from certain how phylogenetic patterns translate to within-species variation in female ornamentation. For example, allelic variation in autosomal genes coding for ornaments will have different effects on the phenotypic correlation between the sexes than variation in sex-linked modifier genes (Fig. 2).

Genetic correlations between the male and the female trait are often presented as an alternative to mutual mate choice (e.g. Muma & Weatherhead 1989; Cuervo et al. 1996). However, models highlight that mutual mate choice may maintain a high genetic correlation between the sexes (Lande 1980). This is probably also true for other types of selection pressures that are similar in magnitude in males and females. Thus, the presence of a genetic correlation between the sexes in a trait does not show that the expression of the trait in females is a consequence of a correlated response to selection in males (Chenoweth & Blows 2003). Studies on mutual ornamentation tend to dismiss genetic correlation as unlikely. An important underlying reason for this is that most models of sexual selection assume some cost to the production or maintenance of the ornament in order to ensure signal honesty (Johnstone 1995; Bradbury & Vehrencamp 1998). Without an associated benefit in females there should thus be strong selection for suppression expression of the trait in females (Sherman & Westneat 1988; Reeve & Sherman 1993, 2002; Amundsen 2000a; Komdeur et al. 2005). This argument assumes that enough time has passed to allow complete sex limitation to evolve. Furthermore, the argument is usually entirely theoretical, as the proposed fitness costs of the ornament are rarely shown.

In summary, convincing support for the genetic correlation hypothesis is currently limited to a single study of an ornament (Price 1996). Nevertheless, we conclude that genetic correlations between the sexes will rarely account fully for mutual ornamentation because of the apparent ease with which taxa switch between sexual monomorphism and sexual dimorphism during the course of evolutionary history. However, we stress that our understanding of the role of genetic correlations in ornament evolution is still limited.

MUTUAL SEXUAL SELECTION

It is evident that female ornaments can have a signal function in species with conventional sex roles, because females of certain species display ornaments that are not present in males (Funk & Tallamy 2000; Amundsen & Forsgren 2001; Domb & Pagel 2001). Such female-specific signals cannot be explained by genetic correlations and, therefore, must be adaptive. It is thus likely that many mutual ornaments also have an adaptive signal function in females, signalling either the same or a different aspect of individual quality as males. For example, Blount et al. (2002) showed that female lesser black-backed gulls, *Larus fuscus*, that were provided with extra carotenoids had brighter legs, bills and orbital rings and also increased maternal health, which resulted in the production of high quality eggs (Blount et al. 2002). Thus the integument brightness of the female reliably signals maternal quality. Males possess the same bright bare parts as females in this species (mutual ornament). While not studied, it seems very likely that male integument coloration and condition are affected by carotenoid intake in the same way as in females, and may thus signal male quality. Table 2 summarizes studies that looked for aspects of fitness that correlate with ornament expression in females or both sexes in a variety of species. The mean Fisher's Z for these estimates was marginally significantly different from zero (mean 0.28, 95% confidence interval: 0.04−0.52), which suggests that signalling aspects of fitness is a general feature of mutual ornaments. As the total heterogeneity was not significant ($Q_{tot,29} = 11.16$, $P = 0.99$), we did not explore whether other factors contributed significantly to the variance in effect sizes. Thus, although most individual studies (65%, $N = 69$) identified at least one fitness correlate of ornament expression, the overall pattern is weak, which is consistent with results for male-specific ornaments (Møller & Jennions 2001). Many of correlations reported in the individual studies are difficult to interpret because there is no a priori reason why the ornament should correlate with one fitness trait and not another. We conclude that despite the relatively large number of studies

Table 2. Data used in the meta-analysis of studies investigating correlations between the level of ornament expression and components of fitness

Species	Scientific name	Ornamental trait[1]	Fitness component	Sex	Age corrected	Reported or estimated r[16]	N	Source
Birds								
Yellow-eyed penguin	*Megadyptes antipodes*	Eye colour[3]	Annual number of fledgling[6]	M	Yes[12]	0.458	36	Massaro et al. 2003
				F	Yes[12]	0.4001	42	Massaro et al. 2003
		Postocular stripe colour[4]	Annual number of fledgling[6]	M	Yes[12]	0.2335	36	Massaro et al. 2003
				F	Yes[12]	0.5315	42	Massaro et al. 2003
Red-tailed tropicbird	*Phaethon rubricauda*	Tail streamer length[5]	Chick body mass[6]	M	Yes[13]	0.6	9	Veit & Jones 2003
				F	Yes[13]	0.3	12	Veit & Jones 2003
			Fledging success[6]	MF	Yes[13]	0.071	72	Veit & Jones 2003
			Laying date[8]	MF	Yes[13]	0.1	152	Veit & Jones 2003
			Residual body mass[7]	MF	Yes[13]	0.03	103	Veit & Jones 2003
Great cormorant	*Phalacrocorax carbo*	Cheek colour[4]	Breeding date[8]	M	No	−0.16	100	Childress & Bennun 2002
				F	No	−0.16	100	Childress & Bennun 2002
		Gular skin colour[3]	Breeding date[8]	F	No	−0.02	100	Childress & Bennun 2002
				M	No	−0.23	100	Childress & Bennun 2002
		Head filoplume length[5]	Breeding date[8]	M	No	−0.21	100	Childress & Bennun 2002
				F	No	−0.21	100	Childress & Bennun 2002
		Suborbital skin colour[3]	Breeding date[8]	F	No	−0.32	100	Childress & Bennun 2002
				M	No	−0.32	100	Childress & Bennun 2002
		Thigh patch colour[4]	Breeding date[8]	F	No	−0.27	100	Childress & Bennun 2002
				M	No	−0.27	100	Childress & Bennun 2002
European shag	*Phalacrocorax aristotelis*	Crest size[5]	Laying date[8]	M	Yes[13]	−0.6	23	Daunt et al. 2003
				F	Yes[13]	−0.57	25	Daunt et al. 2003
Cattle egret	*Bubulcus ibis*	Plume score[5]	Feeding rate[9]	F	No	0.2511	23	Krebs et al. 2004
				M	No	0.5171	23	Krebs et al. 2004
			Fledging success[6]	M	No	0.1741	64	Krebs et al. 2004
				F	No	−0.2424	64	Krebs et al. 2004
			Nest attendance[9]	F	No	0.11	45	Krebs et al. 2004
				M	No	0.0337	45	Krebs et al. 2004
			Nestling attendance[9]	F	No	0.1286	23	Krebs et al. 2004
				M	No	0.0067	23	Krebs et al. 2004
Black swan	*Cygnus atratus*	Curled feather number[5]	Offspring survival[6]	MF	Yes[14]	0.32	22	Kraaijeveld et al. 2004b
			Residual body mass[7]	M	Yes[14]	0.35	67	Kraaijeveld et al. 2004b
				F	Yes[14]	−0.09	80	Kraaijeveld et al. 2004b
Red grouse	*Lagopus lagopus*	Comb brightness/size[2,3]	Worm intensity[10]	M	Yes[12]	0.012	78	Mougeot et al. 2005
				F	Yes[12]	0.164	59	Mougeot et al. 2005
		Plumage colour[2,4]	Worm intensity[10]	M	Yes[12]	0.152	78	Mougeot et al. 2005
				F	Yes[12]	0.188	59	Mougeot et al. 2005
Lesser kestrel	*Falco naumanni*	Rump colour[2,4]	Clutch size[6]	F	Yes[12]	0.05	118	Tella et al. 1997
			Feeding rate[9]	F	Yes[12]	0.1707	15	Tella et al. 1997
			Laying date[8]	F	Yes[12]	−0.02	163	Tella et al. 1997
			Number of fledgling[6]	F	Yes[12]	−0.03	122	Tella et al. 1997
			Number of hatchlings[6]	F	Yes[12]	0.11	103	Tella et al. 1997
		Tail colour[2,4]	Feeding rate[9]	F	Yes[12]	0.2042	21	Tella et al. 1997
Bar-tailed godwit	*Limosa lapponica*	Plumage colour[2,4]	Cestode infection[10]	M	Yes[14]	0	83	Piersma et al. 2001
				F	Yes[14]	0.0938	87	Piersma et al. 2001

Lesser black-backed gull	*Larus fuscus*	Integument brightness[3]	Egg carotenoid[6]	F	Yes[15]	0.522	16	Blount et al. 2002
Inca tern	*Larosterna inca*	Moustache length[5]	Chick body mass[6]	M	No	0.62	12	Velando et al. 2001
				F	No	0.56	21	Velando et al. 2001
			Chick immune response[6]	M	No	0.43	18	Velando et al. 2001
				F	No	0.53	21	Velando et al. 2001
			Residual body mass[7]	M	No	0.033	42	Velando et al. 2001
				F	No	0.4	60	Velando et al. 2001
		Wattle length/colour[3]	Residual body mass[7]	M	No	0.475	42	Velando et al. 2001
				F	No	0.275	61	Velando et al. 2001
Crested auklet	*Aethia cristatella*	Aurical plume length[5]	Residual body mass[7]	M	No	0.18	183	Jones et al. 2000
		Crest length[5]	Residual body mass[7]	F	No	0.23	122	Jones et al. 2000
Least auklet	*Aethia pusilla*	Multiple[5]	Feeding interval[9]	MF	Yes[14]	0.1	170	Jones & Montgomerie 1992
			Feeding rate[9]	MF	Yes[14]	0.167	139	Jones & Montgomerie 1992
			Food deliveries[9]	MF	Yes[14]	0.15	167	Jones & Montgomerie 1992
			Hatching date[8]	MF	Yes[14]	0.12	158	Jones & Montgomerie 1992
			Residual body mass[7]	MF	Yes[14]	0.21	194	Jones & Montgomerie 1992
		Aurical plume length[5]	Return rate[11]	MF	Yes[14]	0.075	412	Jones & Montgomerie 1992
Barn owl	*Tyto alba*	Plumage colour[2,4]	Clutch size[6]	M	Yes[12]	0.1738	152	Roulin et al. 2001a
			Clutch size[6]	F	Yes[12]	0.0973	179	Roulin et al. 2001a
			Hatching date[8]	M	Yes[12]	0.04	158	Roulin et al. 2001a
			Hatching date[8]	F	Yes[12]	0.1939	182	Roulin et al. 2001a
			Nestling feeding rate[9]	M	Yes[12]	0.4448	26	Roulin et al. 2001a
				F	Yes[12]	0.2507	26	Roulin et al. 2001a
			Number of fledglings[6]	M	Yes[12]	0.1162	151	Roulin et al. 2001a
				F	Yes[12]	0.1191	175	Roulin et al. 2001a
		Plumage spottiness[2,4]	Chick body mass[6]	F	Yes[12]	0.5236	30	Roulin et al. 2003
			Feather asymmetry[7]	M	Yes[12]	−0.33	37	Roulin et al. 2003
				F	Yes[12]	0.0052	38	Roulin et al. 2003
			Fledging success[6]	F	Yes[12]	0.28	33	Roulin et al. 2003
			Offspring asymmetry[6]	F	Yes[15]	−0.32	43	Roulin et al. 2003
				M	Yes[15]	−0.11	35	Roulin et al. 2003
			Offspring ectoparasite load[10]	F	Yes[12]	−0.2224	50	Roulin et al. 2001b
Northern flicker	*Colaptes auratus*	Hybrid index[4]	Laying date[8]	M	No	0.32	65	Wiebe 2000
				F	No	0.32	66	Wiebe 2000
Scissor-tailed flycatcher	*Tyrannus forficatus*	Tail length[2,5]	Arrival date[8]	M	Yes[14]	−0.073	6	Regosin & Pruett-Jones 2001
				F	Yes[14]	−0.785	6	Regosin & Pruett-Jones 2001
			Clutch initiation[8]	M	Yes[14]	−0.418	39	Regosin & Pruett-Jones 2001
				F	Yes[14]	−0.154	31	Regosin & Pruett-Jones 2001
Pied flycatcher	*Ficedula hypoleuca*	Forehead patch size[2,4]	*Trypanosome* infection[10]	M	Yes[12]	0.11	40	Potti & Merino 1996
				F	Yes[12]	0.44	8	Potti & Merino 1996
Barn swallow	*Hirundo rustica*	Tail length[5]	Mate acquisition date[8]	F	Yes[12]	0.9816	342	Møller 1993
			Number fledged[6]	F	Yes[12]	0.8471	336	Møller 1993
			Time of arrival[8]	F	No	−0.27	67	Cuervo et al. 1996
Bluethroat	*Luscinia svecica*	Throat colour[2,4]	Body mass[7]	F	Yes[13]	0.34	54	Amundsen et al. 1997
				F	Yes[15]	0.08	27	Smiseth & Amundsen 2000
			Chick body mass[6]	F	Yes[15]	0.63	9	Smiseth & Amundsen 2000
			Clutch size[6]	F	Yes[15]	−0.1	23	Smiseth & Amundsen 2000
			Hatching date[8]	F	Yes[15]	0.17	23	Smiseth & Amundsen 2000
			Nestling feeding rate[9]	F	Yes[15]	−0.22	28	Smiseth & Amundsen 2000
			Residual body mass[7]	F	Yes[15]	0.1	27	Smiseth & Amundsen 2000

(*continued on next page*)

Table 2 (*continued*)

Species	Scientific name	Ornamental trait[1]	Fitness component	Sex	Age corrected	Reported or estimated r[16]	N	Source
Great tit	*Parus major*	Cheek patch[4]	Chick body mass[6]	M	Yes[12]	0.26	57	Ferns & Hinsley 2004
			Laying date[8]	F	Yes[12]	−0.48	70	Ferns & Hinsley 2004
Black-billed magpie	*Pica pica*	Tail damage[5]	Fledging date[8]	M	No	0.0364	10	Fitzpatrick & Price 1997
				F	No	0.301	10	Fitzpatrick & Price 1997
			Nesting date[8]	M	No	−0.3136	11	Fitzpatrick & Price 1997
				F	No	−0.0657	11	Fitzpatrick & Price 1997
			Number of fledglings[6]	MF	No	0.595	13	Fitzpatrick & Price 1997
			Pairing date[8]	M	No	0.81	15	Fitzpatrick & Price 1997
				F	No	−0.5334	15	Fitzpatrick & Price 1997
		Tail PC1[5]	Lice intensity[10]	F	Yes[14]	−0.7	12	Blanco & De la Puente 2002
European starling	*Sturnus vulgaris*	Throat feather PC1[4]	Body mass[7]	M	Yes[12]	0.305	30	Komdeur et al. 2005
				F	Yes[12]	0.097	44	Komdeur et al. 2005
			Clutch size[6]	M	Yes[12]	0.1317	28	Komdeur et al. 2005
				F	Yes[12]	0.1539	46	Komdeur et al. 2005
			Hatching success[6]	M	Yes[12]	0.088	26	Komdeur et al. 2005
				F	Yes[12]	0.121	46	Komdeur et al. 2005
			Incubation[9]	M	Yes[12]	−0.163	17	Komdeur et al. 2005
				F	Yes[12]	0.259	21	Komdeur et al. 2005
			Laying date[8]	F	No	−0.189	45	Komdeur et al. 2005
				M	No	−0.11	27	Komdeur et al. 2005
Rock sparrow	*Petronia petronia*	Breast patch size[4]	Body mass[7]	F	Yes[15]	0.32	39	Pilastro et al. 2003
			Nestling feeding rate[9]	F	Yes[15]	0.605	8	Pilastro et al. 2003
			Number of broods per year[6]	F	Yes[15]	0.0532	44	Pilastro et al. 2003
			Time at nest[9]	F	Yes[15]	−0.977	8	Pilastro et al. 2003
House finch	*Carpodacus mexicanus*	Plumage brightness[2,4]	Clutch size[6]	F	Yes[14]	−0.12	43	Hill 1993b
			Number fledged[6]	F	Yes[14]	−0.12	34	Hill 1993b
			Proportion fledged[6]	F	Yes[14]	−0.06	34	Hill 1993b
			Residual body mass[7]	F	Yes[14]	0.085	41	Hill 1993b
			Return rate[11]	F	Yes[14]	−0.012	70	Hill 1993b
			Timing of breeding[8]	F	Yes[14]	−0.1	80	Hill 1993b
Northern cardinal	*Cardinalis cardinalis*	Bill colour[2,3]	Residual body mass[7]	F	No	0.2244	81	Jawor et al. 2004
		Face mask score[2,4]	Nestling feeding rate[9]	F	No	0.4	23	Jawor et al. 2004
		Underwing colour[2,4]	Feedings/h[9]	F	No	0.24	17	Linville et al. 1998
			Feedings/nestling/h[9]	F	No	0.4	17	Linville et al. 1998
			First nest date[8]	F	No	0.36	34	Jawor et al. 2004
			Number of broods fledged[6]	F	No	0.4796	36	Jawor et al. 2004
			Residual body mass[7]	F	No	0.29	84	Jawor et al. 2004
Red-winged blackbird	*Agelaius phoeniceus*	Epaulette brightness[2,4]	Clutch initiation date[8]	F	No	0.248	87	Muma & Weatherhead 1989
Reptiles								
Agamid lizard	*Ctenophorus ornatus*	UV chroma[4]	Laying date[8]	F	No	−0.52	13	LeBas & Marshall 2000

		Egg number[6]	F	No	−0.17	16		
		Egg weight[6]	F	No	−0.45	9		
Insects								
Stalk-eyed fly	*Cyrtodiopsis dalmanni*	Residual eyespan[2,5]	Food[7]	M	Yes[15]	0.85	267	Cotton et al. 2004
				F	Yes[15]	0.72	266	Cotton et al. 2004
Stalk-eyed fly	*Sphyracephala beccarri*	Residual eyespan[5]	Food[7]	M	Yes[15]	0.99	237	Cotton et al. 2004
				F	Yes[15]	0.92	271	Cotton et al. 2004
Paper wasp	*Polistes dominulus*	Facial pattern[2,4]	Body size[7]	F	No	0.28	127	Tibbetts & Dale 2004

1: weighted means of multiple measurements on the same ornament; 2: ornament sexually dimorphic; *ornament groupings*: 3: integument colour; 4: body colour; 5: structure size; *fitness parameters*: 6: reproductive success; 7: body condition; 8: timing of breeding; 9: parental investment; 10: parasite resistance; 11: survival; *age correction*: 12: statistically; 13: ornament not age-related; 14: analysis restricted to adults; 15: randomized in experiment; 16: multiple estimates (different cohort etc.) combined as weighted means.

reporting a correlation between mutual ornamentation and some component of fitness, there is a need for experiments to test this hypothesis.

The mutual sexual selection hypothesis proposes that elaborate monomorphic characters function in both sexes as mate-choice signals or status signals used during competition for mates, whereby the most ornamented males and females are of highest quality and obtain highest mating success. Male and female competition for mates is expected to occur when the potential reproductive rate is similar for both sexes (Clutton-Brock & Vincent 1991), and when the operational sex ratio is near unity, as neither sex will represent a scarce resource to be competed over by a limited sex (Emlen & Oring 1977). Because the potential reproductive rate and the operational sex ratio are highly dependent on the relative degree of male and female parental investment, mutual sexual selection is expected to operate most strongly on socially monogamous species with obligate biparental care (Burley 1986). A series of game-theoretical models by Johnstone and coworkers (Johnstone et al. 1996; Johnstone 1997; Kokko & Johnstone 2002) showed that mutual mate choice is expected when there is high variance in individual quality among potential mates of both sexes. High quality-variance means that the benefits of choice will be high. Mutual choosiness is further promoted by high mate encounter rates (offering considerable potential for exercising choice), so that rejected mates can be replaced quickly (Johnstone et al. 1996; Kokko & Johnstone 2002). On the other hand, high costs of choice and poor information will hamper mutual choice (Johnstone et al. 1996; Johnstone 1997; Kokko & Monaghan 2001). Interestingly, Kokko & Johnstone (2002) showed that mutual choice is especially likely when breeding is very costly and the benefits of biparental care are synergistic. Mutual ornamentation may thus be relatively common in such situations. Nevertheless, a recent population genetic model showed that male mating preferences can also be maintained in polygynous mating systems, but only if it is based on a trait that indicates high fertility or viability in females, or if it is linked to female mate preference through pleiotropy (Servedio & Lande 2006).

There is now robust experimental evidence that mutual mate choice occurs in a variety of taxa, including birds (Monaghan et al. 1996; Faivre et al. 2001; Sæther et al. 2001), amphibians (Verrell 1995), fish (Rowland 1982, 1989; Kraak & Bakker 1998; Werner & Lotem 2003; Wong et al. 2004), amphipods (Hua Wen 1993), termites (Shellman-Reeve 1999), fruit flies (Chenoweth & Blows 2003) and rotifers (Gómez & Serra 1996). As predicted, males and females both invest in parental care in most of these species. It is currently difficult to assess how widespread mutual mate choice is. Sex-differences in method of mate choice (Shellman-Reeve 1999; Chenoweth & Blows 2003; Santangelo & Itzkowitz 2004) may often make it difficult to recognize mate choice in both sexes.

Table 3 summarizes the experiments that tested for male preference for enhanced ornamentation in females. The mean effect size was significantly different from zero (Fisher's $Z = 0.39$, 95% confidence interval: 0.27−0.54), and these studies thus provide strong support for male

Table 3. Data used in meta-analysis of experimental studies investigating whether mutual ornaments are involved in mate choice

Species	Scientific name	Ornamental trait	Type of manipulation	Response variable	Sex	Reported or estimated r[5]	N	Source
Birds								
Blue-footed booby	*Sula nebouxii*	Foot colour[2]	Colour reduced	Courtship rate	F	0.4458	26	Torres & Velando 2005
Crested auklet	*Aethia cristatella*	Crest length[4]	Lengthened or shortened	Courtship rate	F	0.1877375	322	Jones & Hunter 1993
					M	0.2617375	418	Jones & Hunter 1999
Least auklet	*Aethia pusilla*	Aurical plumes[4]	Enhanced	Courtship rate	M	0.2737	1591	Jones & Montgomerie 1992
		Bill colour[2]			M	0.30445	1130	Jones & Montgomerie 1992
		Bill ornament[2]			M	0.0263	1155	Jones & Montgomerie 1992
Budgerigar	*Melopsittacus undulatus*	Crown fluorescense[3]	Reduced	Attendance rate	F	0.4855	10	Arnold et al. 2002
					M	0.6401	10	Arnold et al. 2002
Barn owl	*Tyto alba*	Plumage spottiness[1,3]	Reduced	Nestling provisioning rate	F	0.4156	33	Roulin 1999
Barn swallow	*Hirundo rustica*	Tail length[4]	Lengthened or shortened	Breeding date	F	0.089	48	Cuervo et al. 1996
Bluethroat	*Luscinia svecica*	Leg band colour[3]	Artificial ornament	Courtship rate	F	0.4168	28	Hansen et al. 1999
		Throat colour[3]	Natural variation	Courtship rate	F	0.460275	13	Amundsen et al. 1997
Bearded tit	*Panurus biarmicus*	Tail length[4]	Lengthened or shortened	Attendance rate	F	0.29555	13	Romero-Pujante et al. 2002
					M	0.60755	12	Romero-Pujante et al. 2002
Blue tit	*Parus caeruleus*	Cap UV[3]	UV blocked	Number of hops	F	0.576	6	Hunt et al. 1999
					M	0.1804	6	Hunt et al. 1999
Pinyon jay	*Gymnorhinus cyanocephalus*	Plumage brightness[3]	Natural variation	Courtship rate	F	0.1167	26	Johnson 1988
Rock sparrow	*Petronia petronia*	Breast patch size[3]	Reduced	Courtship rate	F	0.7012	10	Griggio et al. 2005
			Enlarged	Display rate, parental care	F	0.57688	8	Pilastro et al. 2003
House finch	*Carpodacus mexicanus*	Plumage brightness[1,3]	Enhanced	Preference rank	F	0.8242	13	Hill 1993b
Dark-eyed junco	*Junco hyemalis*	Tail white[3]	Enhanced	Attendance rate	F	0.106	32	Wolf et al. 2004
Red-winged blackbird	*Agelaius phoeniceus*	Epaulette brightness[1,3]	Natural variation	Attendance rate, display rate	F	0.10095	18	Muma &Weatherhead 1989
Reptiles								
Agamid lizard	*Ctenophorus ornatus*	UV chroma[3]	Natural variation	Attendance rate	F	0.3878	18	LeBas & Marshall 2000
Fish								
Three-spined stickleback	*Gasterosteus aculeatus*	Pelvic spine redness[3]	Natural variation	Attendance rate	F	0.526	38	Nordeide 2002
Brook stickleback	*Culaea inconstans*	Body colur[1,3]	Natural variation	Courtship rate, attendance rate	F	0.684495	15	McLennan 1995
Two-spotted goby	*Gobiusculus flavescens*	Belly colour[1,3]	Natural variation	Courtship rate, attendance rate	F	0.7696	16	Amundsen & Forsgren 2001
Insects								
Butterfly	*Pieris occidentalis*	Melanin wing pattern[3]	Natural variation	Courtship rate	F	0.7978	11	Wiernasz 1995
Checkered white butterfly	*Pieris protodice*	Melanin wing pattern[3]	Natural variation	Courtship rate	F	0.6571	10	Wiernasz 1995
		UV reflectance[3]			F	0.5896	40	Rutowski 1982

1: ornament sexually dimorphic; *ornament type grouping*: 2: integument colour; 3: body colour; 4: structure size; 5: weighted means of multiple response variables.

preferences. We found no evidence for publication bias in this sample of studies (Spearman rank correlation: $r_S = -0.08$, $P = 0.69$). The total heterogeneity in effect sizes was not significant ($Q_{tot,19} = 23.86$, $P = 0.20$). Four studies tested for male and female preferences in the same experiment and in three of these, the effect was greater for female preference. While more such experiments are needed for a quantitative analysis, these results suggest that mutual mate preferences based on mutual ornaments may be common. The concomitant prediction of the mutual sexual selection hypothesis is it should result in assortative mating (Trivers 1972). Table 4 lists studies that looked for a correlation between the degree of ornamentation of both partners in a social pair. The mean effect size was significantly greater than zero ($Z = 0.39$, 95% confidence interval: 0.27–0.51). Some caution is required in interpreting this result as there was evidence for publication bias ($r_S = -0.54$, $P = 0.006$). The total heterogeneity in effect sizes was not significant ($Q_{tot,23} = 22.99$, $P = 0.46$). Such patterns are often interpreted as evidence for mutual mate choice. However, this conclusion may not always be justified. For example, Møller (1993) found a positive relationship between the tail length in male and female barn swallows. Subsequent experimentation by Cuervo et al. (1996) found no evidence for mutual mate choice: males did not prefer females with experimentally elongated tails. Theoretically, there are at least four (not mutually exclusive) processes that may result in a pattern of assortative pairing (Burley 1983). (1) Directional mate preferences in both sexes; both sexes prefer to pair with a highly ornamented individual. Highly ornamented individuals would thus obtain highly ornamented partners, leaving less ornamented individuals to pair among themselves (e.g. McLain & Boromisa 1987). If the degree of ornamentation reflects some aspect of individual quality, directional mate preferences should lead to directional selection. (2) Assortative mate preferences in one or both sexes; highly ornamented individuals prefer highly ornamented partners and less ornamented individuals prefer less ornamented partners. This type of mate preference should lead to assortative pairing if one or both sexes are selective and could result in disruptive selection. (3) Convergence of the degree of ornamentation among partners; because partners in a long-term pair bond will tend to occupy a similar physical and social environment, phenotypic plasticity could result in increased resemblance between both individuals over time. (4) Pair formation and ornamentation could both be correlated to a third factor, such as age or arrival date in the breeding area, leading to a positive correlation between ornament size in male and female of a pair (Gimelfarb 1988; Ferrer & Penteriani 2003). Few studies have attempted to distinguish between these mechanisms for assortative mating with regard to a mutual ornament, and those that tried (e.g. Roulin 1999) are unconvincing.

Many ornaments are prominently displayed both before and after pair formation, but their function during the latter stage is poorly understood (Torres & Velando 2005). Dynamic traits (e.g. integument colour, but not feather length) may be used to continually assess a partner's quality and adjust parental investment accordingly. In such situations, high quality individuals may thus elicit enhanced parental care from their partner by displaying an ornament. If both sexes provide care, there would be selection for mutual ornamentation. Recent experiments have shown that male barn owls, *Tyto alba*, and rock sparrows (*Petronia petronia*; both mutually ornamented) adjust their provisioning rate according to their partner's ornamentation, suggesting that mutual ornaments may indeed be used in this way (Roulin 1999; Pilastro et al. 2003; see Table 3). An alternative explanation may be that displaying individuals are trying to attract a secondary mate (e.g. male starlings, Komdeur et al. 2005), or extrapair copulations (many passerine birds). However, this is less likely since many displays are shown by the pair.

In contrast to mutual mate choice, mate competition in both sexes has received little attention (Amundsen 2000b). In species where males provide a nuptial gift, females often compete over access to males carrying large gifts. Studies in crickets have shown that such female–female competition intensifies when food resources are limited and the nuptial gift thus relatively more valuable (Gwynne 1984; Gwynne & Simmons 1990). Female–female competition may also occur in species lacking nuptial gifts. For example, females may reduce the risk of the preferred male being sperm depleted by being the first to mate with that male (Berglund et al. 1993). Observations on leks of several species have shown that such female–female competition is common (Trail 1990; Sæther et al. 2001). In topi antelope, *Damaliscus lunatus*, females use their horns in such contests in the same way that topi males use their horns to compete for the best position on the lek (J. Bro-Jørgensen, personal communication). This may explain why topi are monomorphic, despite their highly polygynous mating system. However, it remains to be tested whether females with larger horns are more dominant than those with smaller horns.

Few studies have addressed the critical prediction made by Trivers (1972), that is, that mutual mate choice is expected when variance in reproductive success is similar in males and females. Kraaijeveld et al. (2004a) measured paternity in a population of black swans, *Cygnus atratus*, a mutually ornamented species. Extrapair paternity was relatively common, but the variance in reproductive success was very similar in males and females. This result may be explained by the fact that cuckolding males were often cuckolded themselves. While this finding poses questions about the function of extrapair paternity in this species, it is consistent with a process of mutual mate choice.

Mutual ornamentation might be prevalent in monogamous mating systems with recurrent mate-sampling. Consistent with this idea, Kraaijeveld (2003) found a positive correlation between the degree of ornamentation and the divorce rate among monomorphic bird species. If a pair splits up after breeding, both male and female need to find a new partner before the next breeding season. Prospecting unpaired individuals will usually have limited information on the relative quality of the potential partners. In species with a high divorce rate, this

Table 4. Data used in the meta-analysis of studies testing for a phenotypic correlation in ornament expression between mates

Species	Scientific name	Ornamental trait[1]	Age corrected	Reported or estimated *r*	*N*	Source
Yellow-eyed penguin	*Megadyptes antipodes*	Eye colour[3]	Yes[7]	0.279	40	Massaro et al. 2003
		Postocular colour[4]	Yes[7]	0.415	40	Massaro et al. 2003
Magellanic penguin	*Spheniscus magellanicus*	Pectoral colouration[4]	No	0.017	119	Forero et al. 2001
Wandering albatross	*Diomedea exulans*	Plumage colour[4]	No	0.458	38	Jouventin et al. 1999
Red-tailed tropicbird	*Phaethon rubricauda*	Tail streamer length[5]	Yes[7]	0.2	57	Veit & Jones 2003
Great cormorant	*Phalacrocorax carbo*	Suborbital skin[3]	No	0.31	100	Childress & Bennun 2002
		Thigh patch[4]	No	0.08	100	Childress & Bennun 2002
		Head filoplumes[4]	No	0.15	100	Childress & Bennun 2002
		Cheek colour[4]	No	0.15	100	Childress & Bennun 2002
		Gular skin colour[3]	No	0.24	100	Childress & Bennun 2002
European shag	*Phalacrocorax aristotelis*	Crest size[5]	Yes[7]	0.44	20	Daunt et al. 2003
Cattle egret	*Bubulcus ibis*	Plume score[5]	No	0.7	135	Krebs et al. 2004
Black swan	*Cygnus atratus*	Curled feather number[5]	Yes[7]	0.61	22	Kraaijeveld et al. 2004b
Ruddy turnstone	*Arenaria interpres*	Plumage colour[4]	No	0.0955	7	Whitfield 1986
Crested auklet	*Aethia cristatella*	Crest length[5]	Yes[8]	0.4713	86	Jones & Hunter 1999
Least auklet	*Aethia pusilla*	Plumage colour[4]	No	0.2964	85	Jones & Montgomerie 1992
		Plume length[5]	No	0.02	54	Jones & Montgomerie 1992
		Auricular plume score[5]	No	−0.35	47	Jones & Montgomerie 1992
		Forehead plume score[5]	No	0.15	46	Jones & Montgomerie 1992
		Bill colour[3]	No	0.01	54	Jones & Montgomerie 1992
		Bill ornamentation[3]	No	0.22	50	Jones & Montgomerie 1992
Barn owl	*Tyto alba*	Plumage spottiness[2,4]	Yes[7]	0.21	132	Roulin 1999
Northern flicker	*Colaptes auratus*	Plumage colour[4]	No	0.35	58	Wiebe 2000
		Nape size[4]	No	−0.08	58	Wiebe 2000
		Hybrid index[4]	No	0.22	58	Wiebe 2000
Scissor-tailed flycatcher	*Tyrannus forficatus*	Tail length[5]	Yes[8]	0.233	27	Regosin & Pruett-Jones 2001
Pied flycatcher	*Ficedula hypoleuca*	Forehead patch size[2,4]	Yes[6]	0.17	53	Potti & Merino 1996
Barn swallow	*Hirundo rustica*	Tail length[5]	Yes[6]	0.2723	338	Møller 1993
Blue tit	*Parus caeruleus*	Cap UV chroma[4]	Yes[7]	0.7	18	Andersson et al. 1998
Great tit	*Parus major*	Cheek patch colour[4]	Yes[6]	0.7	15	Ferns & Hinsley 2004
Black-billed magpie	*Pica pica*	Tail quality[5]	No	0.7	15	Fitzpatrick & Price 1997
European starling	*Sturnus vulgaris*	Throat feather PC1[5]	No	0.754	19	Komdeur et al. 2005
Rock sparrow	*Petronia petronia*	Breast patch size[4]	Yes[7]	0.42	44	Griggio et al. 2005
American goldfinch	*Carduelis tristis*	Plumage colour[2,4]	No	0.55	22	MacDougall & Montgomerie 2003
House finch	*Carpodacus mexicanus*	Plumage brightness[2,4]	Yes[8]	0.22	107	Hill 1993b
Northern cardinal	*Cardinalis cardinalis*	Plumage colour[2,4]	Yes[7]	0.58	22	Jawor et al. 2003
		Bill colour[3]	Yes[7]	0.52	26	Jawor et al. 2003
		Plumage colour[2,4]	No	−0.22	17	Linville et al. 1998

1: weighted mean of multiple measurements on the same ornament; 2: ornament sexually dimorphic; *ornament type grouping*: 3: integument colour; 4: body colour; 5: structure size; *age correction*: 6: statistically; 7: ornament not age-related; 8: analysis restricted to adults.

situation is common and such species may benefit from ornaments that are informative on the quality of the bearer.

NATURAL SELECTION

The conclusion that sexually dimorphic ornament expression is usually achieved through the evolution of modifier mechanisms in females implies that there is strong selection on females against the expression of the ornament in such cases. In support of this idea, Martin & Badyaev (1996) found a negative correlation in females, but not males, between plumage brightness and the frequency of nest predation among species of warblers and finches. Few studies have explicitly quantified the cost of ornament expression for each sex. This is a fruitful area for future research, because sexual dimorphism are expected be a result of differential balances of selective pressures in males and females, rather than the absence of, for example, mate choice in males (Wallace 1889; Stuart-Fox et al. 2003; Langerhans et al. 2005). Northern cardinals, *Cardinalis cardinalis*, illustrate this point. This species is highly sexually dimorphic, with males elaborately ornamented and females much duller. Highly ornamented males are often paired to highly ornamented females (Jawor et al. 2003; but see Linville et al. 1998), suggesting that there may be directional sexual selection favouring female ornaments. The dull plumage of female Northern cardinals is thus likely to be the result of natural selection against brightly coloured females, for example through predation, although this has not been quantified. It is noteworthy that one of the female ornaments preferred by males is brightly coloured underwing feathers, a trait that is hidden under normal circumstances and thus probably less subject to natural selection. Thus, it is possible that species may evolve towards sexually dimorphic ornamentation in spite of similar mate preferences in males and females. A recent model has shown that directional mating preference in males may be maintained when it is balanced by natural selection (Chenoweth et al. 2006). However, the cost of ornament expression in females may actually reduce the benefits of male mate choice. For example, females may face a trade-off between signalling and fecundity because the resources spent on signalling can no longer be allocated to egg production. In such cases males would be selected to discriminate against very 'attractive' females (i.e. females with high signal values; Fitzpatrick et al. 1995). In such a scenario, males should prefer a certain optimal ornament expression in females, while females should continue to prefer the most ornamented male (Chenoweth et al. 2006). Such a pattern was recently described for cuticular hydrocarbon signals in the fruit fly *D. serrata* (Chenoweth & Blows 2005).

In certain systems, natural selection may select directly for mutual ornamentation. For example, bright colours in male and female poison-dart frogs are thought to signal distastefulness in both sexes (Daly & Myers 1967). However, recent evidence has shown that these colours are also involved in mate choice (Summers et al. 1999).

SOCIAL COMPETITION

Potential mates are only one of many types of resources that individuals may compete over with conspecifics. Selection resulting from social competition over nonsexual resources is known as social selection (Crook 1972; West-Eberhard 1979, 1983, 1984, 1991; Tanaka 1996). Examples of nonsexual resources over which there may be strong social competition include food, winter territories (Rohwer 1975; Ekman 1989; Bleiweiss 1992; Kraaijeveld & Dickinson 2001) and hierarchy positions in social groups (Zahavi 1991). Individuals may benefit from displaying exaggerated traits during nonsexual social competition in the same way as during mate competition. Models of 'interacting phenotypes' have shown that if a trait influences the outcome of social interactions in a way that influences the fitness of the bearer, this can result in social selection on that trait (Moore et al. 1997; Wolf et al. 1999). 'Badges of status' are good examples of such traits and should thus evolve in response to the social environment (Rohwer 1975; Whitfield 1987; Savalli 1995; Zuk & Johnsen 2000; Maynard Smith & Harper 2003). Game-theoretical models (Maynard Smith & Harper 1988; Johnstone & Norris 1993) have shown that such badges can be evolutionary stable. Like sexual signals, exaggerated social signals are likely to be costly and, therefore, opposed by natural selection. Tanaka (1996) examined a quantitative genetic model of social signalling, in which the expression of the signal carried a cost and was thus opposed by natural selection, but benefited the signaller because of social selection. The model predicted signal escalation regardless of sex.

Moore et al. (2002) artificially selected males of the cockroach *Nauphoeta cinerea* for increased or decreased social dominance. In addition to a strong response to selection, they found a correlated response in a pheromonal badge of status, which shows that badges of status can evolve in response to selection for social dominance. While the experiment of Moore et al. (2002) only selected on males, there is no reason why the same would not work in females, or in males and female simultaneously.

Social selection is of particular relevance to the study of mutual ornamentation, because competition over nonsexual resources is likely to be more balanced between the sexes than sexual competition. When the sexes experience the same selection pressure, the resulting signal traits are likely to be monomorphic. Table 5 lists studies that investigated whether ornaments had signal function in social competition in females or both sexes. The mean effect size for these studies was significantly greater than zero (Fisher's $Z = 0.39$, 95% confidence interval: 0.25–0.52). The total heterogeneity in effect sizes was not significant ($Q_{tot,17} = 10.68$, $P = 0.87$). As there was no evidence for publication bias (Spearman rank correlation: $r_S = 0.04$, $P = 0.86$), this result shows that elaborate monomorphic ornaments can act as badges of status in both sexes.

The distinction between sexual and nonsexual resources is blurred and many putative cases of social selection may be interpreted as sexual selection. However, rail chicks provide a clear example where a sexual context is ruled out. Newly hatched rail chicks possess brightly coloured

Table 5. Data used in the meta-analysis of studies investigating whether mutual ornaments function as badges of status

Species	Scientific name	Ornamental trait	Response variable	Sex	Age corrected	Reported or estimated *r*	*N*	Source
Black swan	*Cygnus atratus*	Curled feather number[4]	Dominance status	M	Yes[6]	0.258	53	Kraaijeveld et al. 2004b
				F	Yes[6]	0.621	9	Kraaijeveld et al. 2004b
Dusky moorhen	*Gallinula tenebrosa*	Frontal shield size[2]	Dominance status	MF	Yes[8]	0.3479	100	Crowley & Magrath 2004
Ruddy turnstone	*Arenaria interpres*	Plumage colour[3]	Territory quality	M	No	−0.04395	13	Whitfield 1986
Crested auklet	*Aethia cristatella*	Crest length[4]	Dominance status	M	Yes[7]	0.5513	153	Jones & Hunter 1999
				F	Yes[7]	0.4936	87	Jones & Hunter 1999
Least auklet	*Aethia pusilla*	Plumage colour[3]	Approach to model	MF	Yes[7]	0.1414	999	Jones 1990
Anna's hummingbird	*Calypte anna*	Plumage colour[1,3]	Time spent defending food	MF	Yes[7]	0.5709	12	Ewald & Rohwer 1980
Black-chinned hummingbird	*Archilochus alexandri*	Plumage colour[1,3]	Time spent defending food	MF	Yes[7]	0.7543	7	Ewald & Rohwer 1980
Great tit	*Parus major*	Cheek patch colour[3]	Dominance status	MF	Yes[8]	0.7415	17	Ferns & Hinsley 2004
			Territory quality	M	Yes[8]	0.332	41	Ferns & Hinsley 2004
				F	Yes[8]	0.1234	13	Ferns & Hinsley 2004
		Breast stripe width[3]	Dominance status	MF	Yes[5]	0.93	22	Järvi & Bakken 1984
Pinyon jay	*Gymnorhinus cyanocephalus*	Malar feather colour[3]	Dominance status	F	No	0.3816	35	Johnson 1988
European starling	*Sturnus vulgaris*	Plumage spottiness[1,3]	Dominance status	F	Yes[8]	0.263	35	Swaddle & Witter 1995
Harris sparrow	*Zonotrichia querula*	Head plumage darkness[3]	Dominance status	F	No	0.84	22	Watt 1986
				M	Yes[7]	0.08	16	Jackson et al. 1988
				F	Yes[7]	0.34	17	Jackson et al. 1988
White-crowned sparrow	*Zonotrichia leucophrys*	Crown colour[3]	Dominance status	F	Yes[7]	0.5955	39	Fugle et al. 1984
Dark-eyed junco	*Junco hyemalis*	Plumage colour[3]	Dominance status	M	Yes[7]	0.4113	16	Holberton et al. 1989
				F	Yes[7]	0.452	5	Holberton et al. 1989
Northern cardinal	*Cardinalis cardinalis*	Face mask score[1,3]	Aggression	F	No	0.36	22	Jawor et al. 2004
Red-winged blackbird	*Agelaius phoeniceus*	Plumage brightness[1,3]	Aggression	F	Yes[8]	−0.0745	19	Muma & Weatherhead 1989
Stalk-eyed fly	*Cyrtodiopsis dalmanni*	Eyespan[1,4]	Dominance status	M	No	0.5992	30	Panhuis & Wilkinson 1999
				F	No	0.2236	28	Al-khairulla et al. 2003
Carcass beetle	*Coprophanaeus ensifer*	Horn size[4]	Fighting time	M	No	0.483	19	Otronen 1988
				F	No	0.207	23	Otronen 1988
Paper wasp	*Polistes dominulus*	Facial pattern[1,3]	Dominance status	F	No	0.295	61	Tibbetts & Dale 2004

1: ornament sexually dimorphic; *ornament type grouping*: 2: integument colour; 3: body colour; 4: structure size; *age correction*: 5: statistically; 6: ornament not age-related; 7: separate analyses for age groups; 8: randomized in experiment.

bills, head and plumes. As these traits are very conspicuous, it is expected to have some signal function, but as they are only expressed well before sexual maturity, they cannot be the result of sexual selection. Comparative evidence suggests that social competition among chicks plays a role, as ornamented chicks were more common in species with larger clutches and polygamous mating systems (resulting in lower within-brood relatedness; Krebs & Putland 2004).

Another complication in the study of social selection is that the object of social competition may vary between the sexes. For example, female moorhens, *Gallinula chloropus*, compete over access to high quality males (Petrie 1983), while males compete over territories (Petrie 1984). While the object of competition differs between the sexes, both use the red frontal shield above their bills as a badge of status (Petrie 1988; Eens et al. 2000). Experiments in the closely related dusky moorhen, *Gallinula tenebrosa*, have shown that large-shielded individuals are more likely to win aggressive interactions, regardless of their age and sex (Crowley & Magrath 2004).

Although West-Eberhard (1979, 1983) presented a broad integrated theory of social selection, little research has been directed towards testing the combined roles of non-sexual social competition, mate competition and mate choice on trait exaggeration. Partly, we believe, this is because good model systems are hard to identify, and partly because of a historical preoccupation with sexual selection in its narrow sense. The studies discussed here provide a tantalizing glimpse into what seems intuitively a very straightforward process: males and females both compete for resources and, therefore, both benefit from expressing an ornamental badge of status.

SELECTION FOR SEXUAL MIMICRY

Frequent interactions with courting males may sometimes be costly for females in group-living species and cause selection on females to be able to conceal their sex (Burley 1981; Butcher & Rowher 1988). If such selection is strong enough, it could conceivably outweigh the cost of producing an otherwise nonfunctional ornament in females. Thus, some cases of mutual ornamentation may be the result of selection for sexual mimicry. An example is the long-tailed finch, *Poephila acuticauda*, a mutually ornamented species for which Langmore & Bennett (1999) showed that subordinate males were less likely than dominant males to reveal their sex through song when encountering an unfamiliar male that did reveal his sex. The function of the ornaments (including a bright red bill and elongated tail feathers) has not been studied in this species, but it may be possible that females express them to avoid harassment by males. In the damselfly *Ischnura ramburi*, females occur in two colour phases; one of which is bright red and resembles males (Robertson 1985). These male-type females mate only half as often as dull-coloured females, which may give them a frequency-dependent advantage (Robertson 1985). A convincing test in favour of the sexual mimicry hypothesis would include evidence that ornaments are favoured by sexual and/or social selection in the dominant sex only, that harassment is costly for the subordinate sex and that the subordinate sex can avoid harassment by expressing the ornament. Furthermore, the idea still awaits formal theoretical evaluation.

FRAMEWORK FOR THE EVOLUTION OF MUTUAL ORNAMENTATION, PITFALLS AND RECOMMENDATIONS

A commonly overlooked factor in studies investigating quality signalling and mate choice is the effect of age on ornamentation. This problem is of particular relevance to mutual ornamentation because correlative patterns of assortative mating that are often used to infer mutual mate choice can also be explained by age-related ornament expression. Table 6 lists studies that investigated age effects on ornamentation in mutually ornamented species. The mean effect size for these studies was not significantly different from zero (Fisher's $Z = 0.38$, 95% confidence interval: -2.85 to 3.61). The total heterogeneity in effect sizes was not significant ($Q_{\text{tot},19} = 0.024$, $P = 0.99$).Thus, while several individual studies reported strong associations between ornament expression and age, this may not be a general pattern. Nevertheless, relationships between ornamentation and measures of quality or attractiveness may be confounded by differences in age and age-related variables in individual study systems. In study systems where the level of ornamentation is highly correlated with age, the strength of the correlation can make it difficult to separate statistically the relative influences of age and ornamentation on partner choice and fitness variables (Komdeur et al. 2005). The assortative pairing by ornamentation observed in many species (Table 4) may no longer be evident when controlled for age-assortative pairing or vice-versa. However, this prediction is not born out by the meta-analysis. The strength of the correlation between the level of ornamentation of social partners was not significantly influenced by whether or not the investigators accounted for the effects of age ($Q_{b1} = 0.06$, $P = 0.80$). It is also possible that in cases where ornamentation is a good predictor of age, the ornament serves as a signal that individuals use to select mates of a preferred age. For example, in species with biparental care, choosing an older mate may provide direct fitness benefits (Newton 1989). Again, however, this is not supported by the results of the meta-analysis. Whether age is accounted for has little effect on the strength of the correlation between ornamentation and fitness parameters ($Q_{b1} = 0.24$, $P = 0.63$; Table 2).

The results of this review indicate that the evolution of mutual ornamentation is influenced by both the genetic correlation between the sexes and by a variety of current selection pressures. These two processes are intimately related and not mutually exclusive. A genetic correlation between the sexes will hamper the evolution towards sexual dimorphism when selection on males and females is in opposite directions (Lande 1980). A small number of studies shows that this is indeed a realistic explanation for certain ornaments that are expressed in both sexes. However, the generality of this pattern is difficult to assess without

Table 6. Data used in meta-analysis of studies investigating whether the level of ornament expression is correlated with age

Species	Scientific name	Ornamental trait[1]	Sex	Number of age groups	Reported or estimated *r*	*N*	Source
Yellow-eyed penguin	*Megadyptes antipodes*	Eye colour[3]	MF	20	0.3369	83	Massaro et al. 2003
		Postocular stripe colour[4]			0.3207	83	Massaro et al. 2003
Red-tailed tropicbird	*Phaethon rubricauda*	Streamer length[5]	MF	19	0.3	372	Veit & Jones 2003
European shag	*Phalacrocorax aristotelis*	Crest size[5]	M	14	0.31	19	Daunt et al. 2003
			F		0.05	17	Daunt et al. 2003
Black swan	*Cygnus atratus*	Curled feather number[5]	M	2	0.0723	81	Kraaijeveld et al. 2004b
			F		0.3376	87	Kraaijeveld et al. 2004b
Red grouse	*Lagopus lagopus*	Comb size/colour[2,3]	M	2	0.415	78	Mougeot et al. 2005
		Plumage colour[2,4]	M		0.1934	78	Mougeot et al. 2005
		Comb size/colour[2,3]	F		0.156	59	Mougeot et al. 2005
		Plumage colour[2,4]	F		0.108	59	Mougeot et al. 2005
Lesser kestrel	*Falco naumanni*	Rump colour[2,4]	F	6	0.6	204	Tella et al. 1997
		Tail colour[2,4]	F	4	0.2723	155	Tella et al. 1997
Crested auklet	*Aethia cristatella*	Crest length[5]	MF	2	0.1502	594	Jones et al. 2000
		Aurical plume length[5]			0.0942	877	Jones et al. 2000
		Rictal plate height[3]			0.1322	577	Jones et al. 2000
Least auklet	*Aethia pusilla*	Aurical plume length/score[5]	MF	2	0.309	298	Jones & Montgomerie 1992
		Forehead plume score[5]			0.6559	277	Jones & Montgomerie 1992
		Bill colour[3]			0.2579	285	Jones & Montgomerie 1992
		Bill ornament height[3]			0.2144	271	Jones & Montgomerie 1992
Barn owl	*Tyto alba*	Plumage spottiness[2,4]	M	10	−0.001	73	Roulin 1999
			F		0.27	44	Roulin 1999
					0.43	50	Roulin et al. 2001b
Scissor-tailed flycatcher	*Tyrannus forficatus*	Tail length[2,5]	M	3	0.889	66	Regosin & Pruett-Jones 2001
			F		0.8207	68	Regosin & Pruett-Jones 2001
Barn swallow	*Hirundo rustica*	Tail length[5]	M	2	0.8393	500	Møller 1993
			F		0.2146	500	Møller 1993
Bluethroat	*Luscinia svecica*	Throat colour[2,4]	F	2	0.0549	64	Amundsen et al. 1997
					0.133	30	Smiseth & Amundsen 2000
Blue tit	*Parus caeruleus*	Cap UV chroma[2,4]	MF	2	0.2419	41	Andersson et al. 1998
Black-billed magpie	*Pica pica*	Tail length/quality[5]	MF	2	0.478	132	Blanco & De la Puente 2002
European starling	*Sturnus vulgaris*	Throat feather PC1[4]	M	2	0.7905	31	Komdeur et al. 2005
			F		0.8675	21	Komdeur et al. 2005
Rock sparrow	*Petronia petronia*	Breast patch size[4]	M	2	0.0662	43	Pilastro et al. 2003
			F		0.0826	47	Pilastro et al. 2003
House finch	*Carpodacus mexicanus*	Plumage colour[2,4]	F	2	0.874	112	Hill 1993a
Dark-eyed junco	*Junco hyemalis*	Tail white[4]	M	2	0.0475	462	Wolf et al. 2004
			F		0.0794	340	Wolf et al. 2004
Northern cardinal	*Cardinalis cardinalis*	Breast colour[2,3]	M	?	0.253	17	Linville et al. 1998
		Underwing colour[2,3]	F		0.276	14	Linville et al. 1998
Red-winged blackbird	*Agelaius phoeniceus*	Epaulette brightness[2,4]	F	2	0.5714	13	Muma & Weatherhead 1989

1: weighted mean of multiple measurements on the same ornament; 2: ornament sexually dimorphic; *ornament type grouping*: 3: integument colour; 4: body colour; 5: structure size.

further quantitative genetic studies. When selection on ornamentation is in the same direction in males and females, this will maintain a genetic correlation between the sexes. Thus, while a genetic correlation between the sexes is an important component of the evolution of mutual ornamentation, the finding of a genetic correlation between the sexes in itself reveals little about the underlying evolutionary process. The relative importance of genetic correlation and current selection in individual systems is difficult to predict a priori. Important insights can be gained from studies of the developmental basis of mutual ornaments. When the development of an ornament is known, it may often be possible to pinpoint the stage where the process in females is uncoupled from that in males in dimorphic species (Emlen et al. 2005a).

In contrast to the poor state of knowledge concerning the genetic correlation between the sexes, there is convincing evidence that mutual ornamentation can be maintained through selection on both sexes. However, the various selection pressures that can influence mutual ornaments have received very different amount of scrutiny. Most studies focus on the role of mutual mate choice. This process now has a good theoretical underpinning and is well supported in a variety of taxa. Nevertheless, most evidence is currently limited to single-species studies. On an interspecific level, much remains to be learned. Most comparative studies that looked for correlates of sexual dimorphism fail to make the distinction between 'bright monomorphic' (mutually ornamented) and 'dull monomorphic'. There is thus much scope for comparative studies that assess the contribution of factors such as ecology and mating system to the evolution of mutual ornamentation.

We suggest that the interest in mutual sexual selection has lead to an overemphasis on mate choice and an underappreciation of the role of other selective pressures such as nonsexual social competition, predation, and sexual mimicry. The present review covers a wide range of topics and while we have tried to be comprehensive, we may have missed some relevant studies. Also, it is possible that meta-analyses using different selection criteria than ours result in important insights. We thus encourage more focused meta-analyses of some of these topics.

Besides a bias in research focus, there is also a bias in the choice of study organism. Current studies on mutual ornamentation are strongly biased to nonpasserine birds. Usually, these species were chosen because they were being studied for other reasons, rather than because they are mutually ornamented. The study of mutual ornamentation is then an afterthought, which does not enhance the rigour of such studies. Some of the most striking examples of mutual ornamentation in birds occur in tropical passerines, yet these species remain poorly studied. Furthermore, mutual ornamentation is common in other taxa, such as cichlid fish, poison-dart frogs and stalk-eyed flies. The opportunities for detailed within-species studies and broad comparative work are thus plentiful.

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